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16. ABSTRACT

The spawing behavior of the Atlantic silverside, *Menidia menidia*, was studied at two sites on the North Edisto River estuary in South Carolina. Spawning *M. menidia* deposited their eggs on three types of substrates including: (1) the lower stems of cordgrass plants, *S. alterniflora*, (2) detrital mats and, (3) exposed cordgrass roots along erosional scarps. Spawing behavior during egg deposition and fertilization was similar for all three spawning substrates. Females released eggs by a rapid fluttering motion of the posterior half of the body. A similar movement accompanied release of milt by males. Behavior of fish just prior to spawning was modified to insure deposition of eggs at locations that provided protection from thermal and desiccation stresses.

During spawning runs in which eggs were deposited at the base of cordgrass plants, ambient dissolved oxygen levels were sometimes reduced to less than 1.0 mg/l. Spent fish, which apparently incurred and oxygen debt while spawning, formed a non-schooling aggregation offshore from the spawning zone.

The availability of suitable spawning substrate influenced the location of spawning runs. Recurring use of certain areas for egg deposition resulted in an uneven distribution of spawning runs along the shoreline at each study site.

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Reproductive behavior of the Atlantic silverside, *Menidia menidia* (Pisces, Atherinidae)*

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Intertidal, Estuaries, Fish, Spawning, Substrates, Dissolved oxygen

Synopsis

The spawning behavior of the Atlantic silverside, *Menidia menidia*, was studied at two sites on the North Edisto River estuary in South Carolina. Prespawning schools moved back and forth along the shoreline as the time of high tide approached. Spawning runs took place in the upper intertidal zone at high tide.

Spawning fish deposited their eggs on three types of substrates: 1) the lower stems of cordgrass plants, *Spartina alterniflora*, 2) detrital mats, and 3) exposed cordgrass roots along erosional scraps. Spawning behavior during egg deposition and fertilization was similar for all three substrates. Females released eggs during a rapid fluttering motion of the posterior half of the body. A similar movement accompanied release of sperm by males. Behavior of fish just prior to spawning insured deposition of gametes at locations that provided protection from thermal and drying stress during development. Eggs were deposited at mean intertidal elevations of 1.8 and 1.5 meters above mean low water (MLW) at respective study sites. They were exposed to the atmosphere for approximately ten hours between successive high tides.

During spawning runs in which eggs were deposited at the base of cordgrass plants, ambient dissolved oxygen concentrations of the water in the spawning area were sometimes reduced to $< 1.0\ mg \cdot l^{-1}$. Spent fish, apparently incurring an oxygen debt while spawning, formed a nonschooling aggregation offshore from the spawning zone.

The recurrent use of specific spawning substrates for egg deposition resulted in an uneven distribution of spawning runs along the shoreline at each study site.

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Introduction

The Atlantic silverside, *Menidia menidia*, an intertidal spawner, is one of the most common fishes found in East Coast estuaries (De Sylva et al. 1962, Dahlberg 1972, Cain & Dean 1976). Its geographic range extends from the Magdalen Islands, Quebec,

Canada (Cox 1921) to northern Florida (Gosline 1948, Johnson 1975).

Menidia menidia spawns seasonally, March through July at southern latitudes and April or May through July at northern latitudes (Nichols 1908, Kuntz & Radcliffe 1918, Hildebrand 1922, Bayliff 1950, Rubinoff & Shaw 1960, Middaugh & Lempesis 1976) in the upper intertidal zone. Goode (1884) provided the following description of a spawning run: 'The fish came in a body into shallow water, within three feet of the shore, then darted among the grass, and rolled over from one side to the other, struggling with all their strength, some of them jumping entirely out of the water (...) The number of fish engaged in spawning was so great that the water was quite whitened with milt, and the grass was so full of the eggs that they could be taken up by the handful.' (See also Fowler 1918 and Hilderbrand 1922).

Little, however, is known about the detailed behavior of *M. menidia* just prior to, during, and immediately after spawning. This report describes the reproductive behavior of *M. menidia*, identifies and characterizes spawning substrates, and the distribution of spawning runs in the North Edisto River estuary during 1976 through 1978 (Middaugh 1981).

Materials and methods

Study sites

The Bears Bluff site, Wadmalaw Island (32°38′42″ lat., 80°15′18″ long.), and Point of Pines site, Edisto Island (32°35′12″ lat., 80°13′48″ long.), are located on the North Edisto River estuary in lower South Carolina. A topographic survey was conducted at each of the study sites. A baseline was established parallel to shore in the upper intertidal zone and wooden stakes driven into the substrate at 3 m intervals. Vertical elevation measurements were made landward and seaward from each baseline stake. Topographic maps (0.4 m elevation intervals) were prepared from the measurements. Concurrent notes were taken on the occurrence of cordgrass, *Spartina alterniflora*, so its distribution in the intertidal zone could be delineated on the maps.

Observations for spawning runs were made for at least 1 h before to 1 h after >90% of the daytime high tides at the study sites during March or April through July of 1976 through 1978. Intertidal elevation and location of maximum egg deposition along the shoreline was noted for most runs.

On several occasions, a portable dissolved oxygen meter was used in measuring oxygen concentrations of water in the spawning zone.

Spawning behavior

Observations were made to determine: 1) the behavior of prespawning schools during a period of 30 to 60 minutes before high tide and the onset of a spawning run, 2) the behavior of schooling and individual *M. menidia* during a spawning run, with special emphasis on spawning substrates and tactics used for egg deposition, and 3) behavior of individuals and aggregations of fish immediately after spawning had taken place.

Results

Prespawning behavior

A specific sequence of events occurred prior to a spawning run. Beginning 30 to 60 minutes before a spawn, a single large school or several small schools of *M. menidia* appeared 10 to 30 m offshore, adjacent to the spawning areas. The schooling fish swam parallel to the shoreline, and gradually moved shoreward as the time of high tide approached. Approximately 15 to 20 minutes prior to spawning, the school moved to within 2 to 3 m of shore and swam back and forth along a 100- to 200 m section of shoreline.

As the school moved along the shoreline, there was a continuous change in the position of fish as individuals overtook other members of the school and moved into a leading position from the offshore lateral flank. Individuals on the inshore side of a school did not appear to move into a leading (forward) position.

After making a pass along the shoreline where cordgrass, detrital mats, or abandoned crab burrows were located, the school would reverse itself, disappearing from the surface momentarily, then begin moving back along the shoreline. Following a

reversal of direction, individuals farthest offshore in the school again moved from their position near the offshore lateral flank of the school to a leading position. If a slight promontory (such as cordgrass projecting into the intertidal zone) was encountered, the leading fish would swim around the promontory and turn inshore, maintaining a position 2 to 3 m offshore.

Spawning behavior

Near the time of high tide, a spawn was initiated by several fish moving into the uppermost intertidal zone. Spawning *M. menidia* deposited their eggs near the base of cordgrass plants, in detrital mats, or in burrows abandoned by the mud crab, *Panopeus herbstii*, and fiddler crab, *Uca pugilator*, along eroding intertidal scarps (15 to 100 cm height).

Individuals that utilized cordgrass as a spawning substrate seemed to prefer areas where the vegetation was positioned so that free movement of a school into (over) the cordgrass at high tide was possible. *M. menidia* spawned in cordgrass that was near the water's edge and covered to a depth of 0 to 30 cm. Ripe females swam between individuals stems of a cordgrass plant, in a position near to, but slightly above, the substrate surface. As the female crossed the axis of the cordgrass, a very rapid fluttering of the body, exaggerated near the tail, was associated with release of mature ova (Fig 1a). On several occasions, males were observed to follow the path of females across the axis of the cordgrass plants, suggesting a pairing of spawners. Males released sperm as they crossed the area of the cordgrass plant where eggs had been deposited (Fig. 1b). Release of sperm by males was also accompanied by rapid fluttering, but the movement of the posterior portion of the body did not seem as vigorous as observed in females. Threads which formed just prior to or during release of ripe ova quickly adhered to the base of the cordgrass plants, thus anchoring the eggs in a position above the substrate yet low enough on the plant to be partially shaded from direct sunlight (Fig. 1c).

A variation of the spawning behavior utilized by *M. menidia* for deposition of eggs in the axis of cordgrass was observed during several spawning runs in 1978. A group of 6 to 15 male fish was observed to maintain a rosette-like position around the base of a cordgrass plant, each positioned so that its head was close to the axis of the plant and its body angled away at a 30 to 45° angle. A procession of up to 12 females swam up through the axis of the plant. Vigorous body movements indicated that each female was depositing eggs on the cordgrass plant as the head and pectoral fins protruded above the surface.

Often, *M. menidia* used detrital mats positioned within or overlying cordgrass plants in the upper intertidal zone as a spawning substrate. Detrital mats at both sites consisted of irregularly shaped particles of decomposing cordgrass that had a surface area of approximately 0.5 to 5.0 mm^2. The detrital particles were similar in appearance to those described by Odum & Cruz (1967) as the 'coarse fraction' retained by a No. 6 plankton net (74 meshes per inch; 0.239 mm aperture). Males and females swam into the detrital mat at a level of 2 to 4 cm below the surface of the semifluid mat and surface of the water (Fig. 2a). Females then turned upward and released their ova by the same rapid fluttering motion of the body observed among females spawning in the axis of cordgrass plants. The females, protruding from the detrital mat so that the pectoral fins could be seen, deposited ova 2 to 3 cm below the surface of the mat (Fig. 2b). Males released sperm as their heads emerged from the detrital mats. Spawning in detrital mats seemed to be indiscriminate. We did not observe pairing of individual males and females.

Movement of *M. menidia* through the detrital mats resulted in an apparently uniform distribution of embryos in the mat. The threads that developed during spawning bound the detrital-embryo mats into a cohesive incubation substrate (Fig. 2c).

In addition to spawning on cordgrass plants and in detrital mats, *M. menidia* often spawned in locations in the upper intertidal zone where scarps had been formed by erosion. Exposed cordgrass roots in abandoned burrows of mud crabs, *Panopeus herbstii*, and fiddler crabs, *Uca pugilator*, were used as spawning substrates along these eroding scarps (Fig. 3a). Mature fish approached the scarps at a depth of 10 to 30 cm below the water's surface. Spawning began as females swam up through a crab burrow, depositing eggs in cordgrass roots that

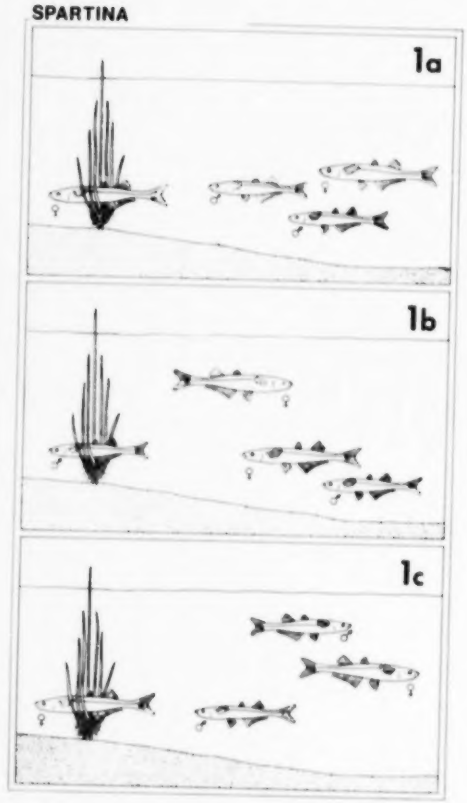

Fig. 1. Menidia menidia utilizing cordgrass, *Spartina alteriflora*, as a spawning substrate: *a* - female deposits eggs at base of plant, *b* - male fertilizes eggs as first female moves offshore, *c* - second female deposits eggs, first spawning pair moves offshore. An apparent pairing of individual males and females was observed on several occasions.

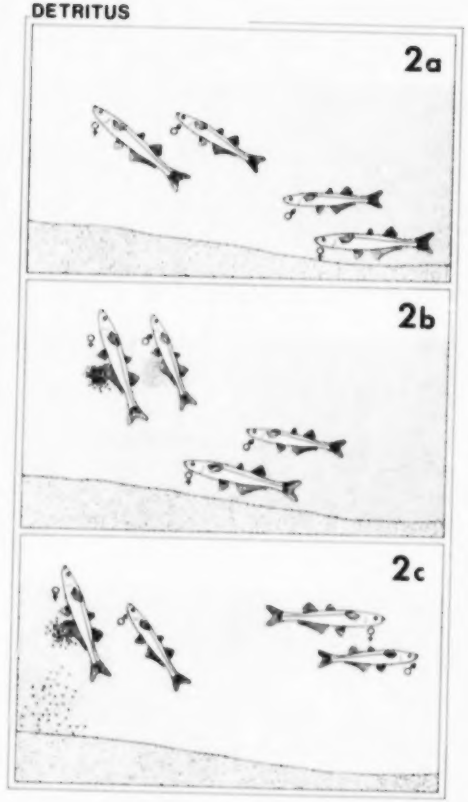

Fig. 2. Menidia menidia spawning in a detrital mat: *a* - males and females swimming through semifluid mat, *b* - deposition of eggs and sperm, *c* - spent fish move offshore as ripe female deposits eggs, male will spawn as head protrudes from detrital mat. No pairing of individual males and females was observed.

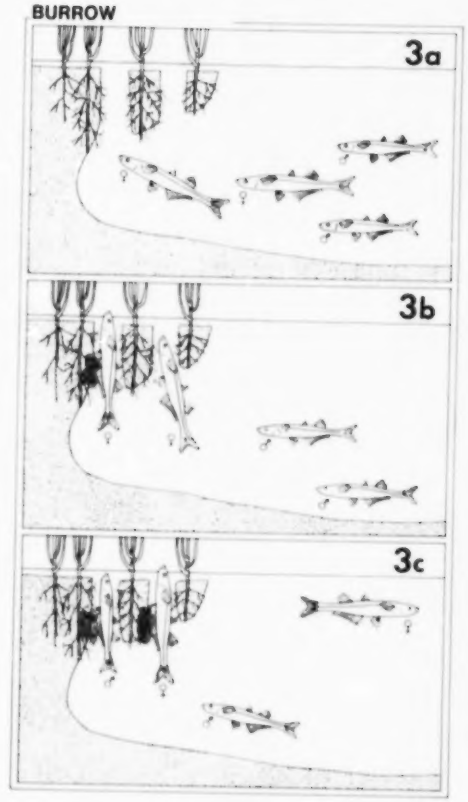

Fig. 3. Menidia menidia spawning in abandoned crab burrows along eroding scarps: *a* - fish approach submerged overhanging scarp, female swims toward crab burrow, *b* - first female deposits eggs on exposed cordgrass roots as second female enters burrow, *c* - male fertilizes eggs as second female spawns. No pairing of individual males and females was observed.

were exposed on the lower portions of the scarp (Fig. 3b). After depositing eggs, females continued to move upward through the crab burrows, exiting through the surface opening in the burrow that had originally served as an entrance when occupied by a crab. Males and additional females then moved upward through the burrow, depositing milt and eggs in the exposed cordgrass root system (Fig. 3c).

Depletion of dissolved oxygen during spawning

Large numbers of *M. menidia* often spawned in a very limited area of cordgrass that ranged from 1 m^2 up to 5-10 m^2. During a heavy spawning run on 30 April 1976 at the Point of Pines, behavior of fish immediately after they had spawned suggested that dissolved oxygen may have become depleted in the spawning area.

Subsequent measurements of dissolved oxygen at a depth of 10 cm below the water's surface were made during a spawning run on 31 May 1976 at the Points of Pines. During the spawning run, dissolved oxygen was reduced from an ambient concentration of about 6 • l^{-1} to <1.0 mg • l^{-1} (Fig. 4). Spawning *M. menidia* were most concentrated in areas with the lowest dissolved oxygen.

Immediately after spawning, spent fish, which remained at the airwater interface, swam to a position 10 to 15 m offshore and formed a tightly grouped aggregation. No schooling was evident.

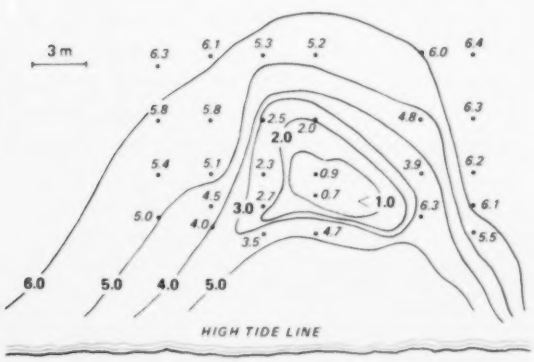

Fig. 4. Dissolved oxygen isopleths for a spawning run observed on 31 May 1976 at the Point of Pines. Values are mg • l^{-1} dissolved oxygen measured 10 cm below the surface. From Middaugh (1981).

Menidia menidia maintained an offshore aggregation while spawning continued inshore, but quickly disappeared from surface waters after the spawning run had ended (Fig. 5).

Prior to several heavy spawning runs, *Pomatomus saltatrix*, and *Cynoscion nebulosis*, were observed preying upon schooling *M. menidia*. During the spawning run of 31 May 1976, these predators were excluded from the spawning zone. Small *P. saltatrix* appeared to penetrate no further than the 4 mg • l^{-1} isopleth, while *C. nebulosis* moved inshore to a position corresponding to the 2.5 to 3.0 mg • l^{-1} isopleth. No predacious fish were observed in the area of most intense spawning and lowest dissolved oxygen.

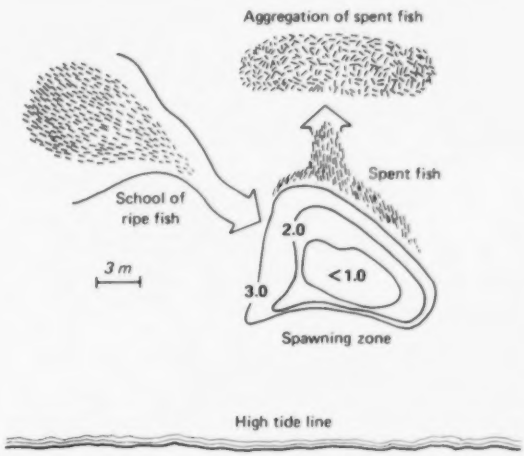

Fig. 5. Summary of movement of fish during spawning run of 31 May 1976. School of ripe fish approached shore, dissolved oxygen concentrations were reduced to <1.0 mg • l^{-1} in the center of the spawning zone. Spent fish then moved offshore from the spawning zone and formed a nonschooling aggregation.

Spawning locations

The intertidal elevation and location along the shoreline of most spawning runs were recorded during 1976-1978. The position of spawning runs at each site apparently was related to the location of suitable spawning substrates, including cordgrass, detrital mats, or erosional scarps. During spawning runs at Bears Bluff, eggs were deposited higher in

the intertidal zone ($\bar{X}$ elevation 1.8 m above MLW, range 1.4-2.4 m, N=37) than at the Point of Pines ($\bar{X}$ elevation 1.5 m, range 1.2-2.0 m, N=61). Embryos at Bears Bluff were exposed to the atmosphere for an average of 10.5 h, for the Point of Pines 9.8 h.

At Bears Bluff, most spawning runs took place on slight promontories. The total number of spawns occurring at given locations within the intertidal zone is shown in Figure 6a, which was divided into five sections of 30 m each for statistical analysis and discussion. Multiple spawns in Section 1 resulted because of the occurrence of tall cordgrass plants used as a substrate. Spawning runs in Section 5 took place because of the presence of tall cordgrass plants as well as detrital mats in the intertidal zone. A χ^2 test of the observed and expected distribution of spawns along the shoreline at Bears Bluff, that assumed an even distribution of spawning runs, indicated a significant difference in use of the sections ($\chi^2 = 30.87$, $P < 0.005$).

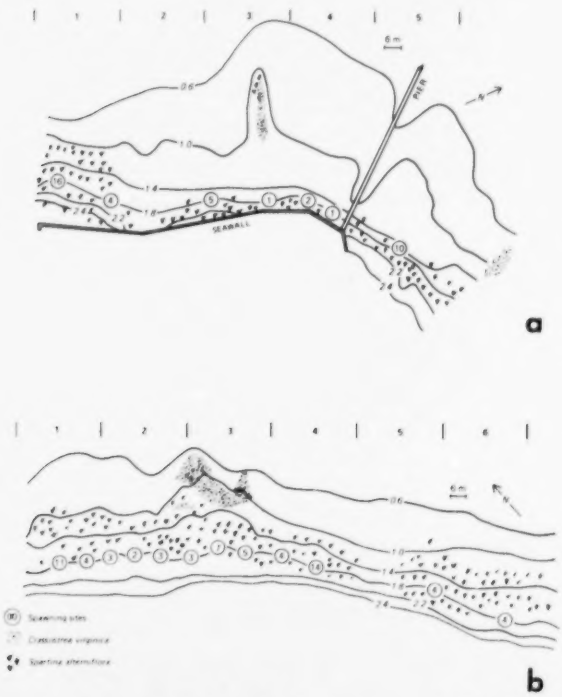

Fig. 6. Topographic maps of study sites: *a*- Bears Bluff, *b*- Point of Pines. Shoreline at each study site was divided into 30 m section for χ^2 analysis. Values inside circles 7 indicate number of spawning runs at each location.

Spawning runs were more uniformly distributed at the Point of Pines. Occurrence of tall cordgrass plants, detrital mats, or eroding scarps resulted in spawning runs along the entire shoreline (Fig. 6b). Extensive use of Sections 1, 3, and 4 occurred because of the respective presence of tall cordgrass, detrital mats, and an eroding scarp. An even distribution of spawning runs also was assumed for the Point of Pines shoreline and a significant difference in use of the sections was observed: $\chi^2 = 16.01$, $P < 0.025$.

Discussion

Schooling *Menidia menidia* approached the shoreline near the spawning site 30 to 60 minutes before the time of high tide. Just before the onset of a spawning run at high tide, *M. menidia* swam along the uppermost part of the intertidal zone until a suitable spawning substrate was encountered. A few fish usually began to spawn at a specific location, and other fish then moved into the spawning zone. Similar observations on prespawning behavior have been made for several intertidal spawners, including *Leuresthes tenuis* (Walker 1949, 1952), *Leuresthes sardina* (Thompson & Muench 1976), and *Galaxias maculatus* (Benzie 1968). Each species seemed to be testing the substrate for spawning during a brief period just before initiation of a spawning run.

Severe depletion of dissolved oxygen concentrations during heavy spawning runs with cordgrass as a substrate for egg attachment probably resulted from utilization of an optimal spawning location by many thousands of individuals. Recently, Johannes (1978) pointed out that several schooling fishes are easily approached and captured while on the spawning grounds. These fish, he stated, seem to exhibit a kind of spawning stupor. In our study, during very heavy spawning runs, *M. menidia* also behaved as if in a spawning stupor, especially during the period immediately after spawning, when they formed nonschooling aggregations just offshore from the spawning zone. On the basis of observations with *M. menidia*, it seems possible that spawning stupor in other fishes could result from depressed dissolved oxygen concentrations on the spawning grounds.

Decreases in dissolved oxygen from ambient

concentrations of about 7 mg • l^{-1} to 5 mg • l^{-1} have been measured in large schools of *Mugil cephalus*. McFarland & Moss (1967) attributed the behavior of individuals within schools of *M. cephalus* to differing dissolved oxygen concentrations present in different areas of the school. In locations with high dissolved oxygen concentrations in the front half and along the sides of the school, fish were densely packed and parallel, whereas in the center and toward the rear of the school, fish were less parallel or entirely unpolarized and actively roiling the surface of the water.

Behavior of schooling *M. menidia* during spawning runs in which dissolved oxygen was reduced showed several similarities to the behavior of schooling *M. cephalus*. For example, *M. menidia* maintained a parallel schooling formation during prespawning movements along the shoreline. Schooling fish in parallel orientation moved into the spawning zone where dissolved oxygen concentrations were depressed. After spawning, *M. menidia* moved in an offshore direction. Individuals showed a less than parallel orientation when moving offshore; their behavior was analogous to that described by McFarland & Moss (1967) for *M. cephalus* near the center of a large school. Formation of a nonschooling aggregation in *M. menidia* and positioning of individuals at the air-water interface are similar to the behavior of *M. cephalus* in the back one third of the school where fish were completely unpolarized (aggregated). Individual *M. cephalus* appeared to rise to the surface, then retreat. Individual *M. menidia* remained at the surface until the spawning run was completed, then disappeared.

Utilization of cordgrass, detrital mats, or abandoned crab burrows along eroding intertidal scarps as spawning substrates by *M. menidia* helped reduce the likelihood of temperature and desiccation stress (Middaugh, unpublished data). Use of cordgrass as a spawning substrate by *M. menidia* parallels descriptions by Hefford (1931) and Benzie (1968) for the catadromous *Galaxias maculatus*. It deposits eggs among the stems and fibrous roots of plants in the upper intertidal zone where they remain cool and moist. Thompson & Thompson (1919) also found that eggs of *Leuresthes tenuis*, which are deposited in a sand substrate in the upper intertidal zone, remained relatively moist even though they had not been inundated for several days.

Spawning site specificity has been reported for several other intertidal fishes. *Fundulus heteroclitus* may utilize filamentous algae (Pearcy & Richards 1962), empty shells of the Atlantic ribbed mussel *Geukensia demissus* (Able & Castagna 1975), or the primary leaves of cordgrass *Spartina alterniflora*, as spawning substrates (Taylor et al. 1977, 1979). Each substrate apparently provided protection from thermal stress as well as predation.

Deposition of eggs by *M. menidia* at elevations from 1.2 to 2.4 m above MLW reduced the time on each tidal cycle for exposure to aquatic predators. Only the blue crab, *Callinectes sapidus*, was observed to consume eggs on high tides (Middaugh 1981).

During low-tide exposure, several birds, including the Ruddy turnstone, *Arenaria interpres morinella*, and semipalmated sandpiper, *Ereunetes pusillus*, were observed to feed on *M. menidia* embryos (Middaugh 1981). However, only embryos located near the base of cordgrass plants or on the surface of detrital-embryo mats were consumed.

In summary, spawning runs of *M. menidia* apparently are timed and located to maximize the likelihood for successful fertilization and incubation of eggs. Severe depletion of dissolved oxygen often occurs during spawning runs. The location of spawning runs within the intertidal zone and along the shoreline apparently was influenced by the occurrence of suitable spawning substrates. Specific substrates were used for egg deposition; each provided protection from temperature and desiccation stress as well as predation.

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